OCCASIONAL PAPERS

of the
MUSEUM OF NATURAL HISTORY
The University of Kansas
Lawrence, Kansas

NUMBER 134, PAGES 1–23 MARCH 8, 1990

SYSTEMATICS OF FROGS OF THE *HYLA LARINOPYGION* GROUP

By

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Stream-breeding hylid frogs of the genera *Hyla*, *Plectrohyla*, and *Ptychohyla* are abundant and rich in species in the highlands of Mexico and Central America (Duellman, 1970). In contrast, only *Hyla* is represented in the Andes, and until recently comparatively few species have been known. These include four species in southern Peru and Bolivia (*H. armata*, *balzani*, *callipleura*, and *melanopleura*) and 12 species in the *Hyla bogotensis* group ranging from Venezuela to Peru, plus one species in Costa Rica and Panama (Duellman, 1972, 1989). The other stream-breeding frogs in the Andes all seem to represent a monophyletic group that has been referred to as the *Hyla larinopygion* group.

The first of these frogs was discovered in 1971 in the Cordillera Central in Colombia and was named as *Hyla larinopygion* (Duellman, 1973). Another species, *Hyla lindae*, was named from the Cordillera Oriental in Ecuador (Duellman and Altig, 1978). Two other species were discovered subsequently—*Hyla pantosticta* from the Cordillera Oriental in southern Colombia and Ecuador (Duellman and Berger, 1982) and *Hyla sarampiona* from the Cordillera Occidental of Colombia (Ruíz and Lynch, 1982). With the exception of *H. larinopygion* in the Cordillera Central in Colombia, frogs in this group are poorly represented in collections. Perhaps this is because of their proclivity to inhabit cliffs in the vicinity of waterfalls, where, even if males

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are calling, their voices do not carry far, and the frogs are difficult to locate.

Our field studies in the Andes of Ecuador have revealed the existence of three more unnamed species in the *Hyla larinopygion* group; furthermore, we obtained frozen tissues of five species in the group. This material, plus a paratype of a new species from the Cordillera Central of Colombia being named by Pedro M. Ruíz, constitutes the basis for this paper, in which we (1) define the *Hyla larinopygion* group, (2) describe three new species, (3) provide a key to the species in the group, and (4) present an hypothesis of the phylogenetic relationships among the species.

MATERIALS AND METHODS

The museum specimens examined are listed with the standardized acronyms (Leviton *et al.*, 1985). Measurements and definitions of external features and osteological characters follow Duellman (1970). Tadpoles were staged according to Gosner (1960).

Tissues were collected for allozymic analysis from five species of the *Hyla larinopygion* group. In addition to those specimens listed in Appendix 1, tissues were obtained from one specimen of *H. larinopygion* (Juan M. Renjifo field number JMR 2072 from Finca La Carelia, Município de Salento, Departamento de Quindio, Colombia; specimen to be deposited in collection of INDERENA, Bogotá, Colombia). Because outgroup relationships of the *Hyla larinopygion* group are poorly understood, we selected representatives from 11 Central and South American species groups of *Hyla* for use as outgroups (Table 1).

Tissue samples (skeletal muscle and livers) were removed from freshly killed frogs and frozen immediately in liquid nitrogen for transport to the laboratory. Tissues were stored for up to three years at -80°C. Tissues were homogenized in ground-glass grinding tubes and diluted 1:1 with 0.01 M tris-0.001 M EDTA-0.001 M 2-mercaptoethanol, pH 7.5. Homogenates were centrifuged at 7000 *g* for 3 min, and the supernatants were refrozen at -80°C prior to use.

Procedures of starch-gel electrophoresis, including buffer recipes and histochemical staining protocols, were the same as described by Hillis (1985). Eighteen genetic loci were scored among species (Table 2). Corrected Nei's genetic distances were calculated as described by Hillis (1984). A UPGMA phenogram of genetic distances was calculated (Sneath and Sokal, 1973) in order to assess average genetic divergence among the species.

The most parsimonious cladogram was constructed from the allozymic data using the procedure described by Hillis (1985). Specifically, any electromorphs that were found in the ingroup and in any of the outgroups were considered to be symplesiomorphies. Electromorphs were ordered into

TABLE 1. Outgroups, collection localities, and informative loci.

Species	Species Group	Provenance	Informative Loci
H. alytolylax	*bogotensis*	Ecuador	EST, LDH-1, LDH-2, MDH-2
H. carnifex	*columbiana*	Ecuador	GPI
H. granosa	*granosa*	Peru	EST, PEP-S, PGM
H. labialis	*labialis*	Colombia	AAT-2, IDH, MDH-2, ME
H. leali	*minima*	Peru	EST, GPI, IDH, PEP-A
H. leucophyllata	*leucophyllata*	Peru	AAT-2, IDH, ME, PEP-A
H. parviceps	*parviceps*	Peru	AAT-2, GPI, MDH-1, PEP-A, PEP-S, PGM
H. pentheter	*bistincta*	Mexico	MDH-1, ME, PEP-A, PEP-S, PGM
H. picturata	*geographica*	Ecuador	IDH, MDH-1, PEP-A, PEP-S
H. rhodopepla	*microcephala*	Peru	AAT-2, GPI, IDH, PEP-A
H. rosenbergi	*boans*	Ecuador	AAT-2, IDH, ME, PEP-A, PEP-S

transformation series following the taxonomic outgroup and functional outgroup criteria of Watrous and Wheeler (1981), as expanded by Farris (1982). Derived electromorphs were considered to be synapomorphies even if they were not fixed within the lineage in which they first appeared.

TAXONOMY

Frogs of the *Hyla larinopygion* group are characterized by (1) large size (snout-vent length to 77.3 mm); (2) large hands and feet with large terminal discs and little webbing; (3) skull well ossified with extensively ossified sphenethmoid and small frontoparietal fontanelle (Fig. 1A); (4) quadratojugal present; (5) vomerine odontophores long, transverse, posterior to choanae, abutting medially (Fig. 1B); (6) prepollical tubercle supported by broad, elliptical, ossified prepollex (Fig. 1C); (7) tadpoles large (up to 80 mm total length) with long, muscular tails; (8) larval mouth ventral with one or two complete rows of marginal papillae and as many as eight upper and ten lower rows of denticles.

The known members of the *Hyla larinopygion* group occur along high-gradient streams in cloud forest at elevations of 1900–2700 m on the slopes

TABLE 2. Loci examined, Enzyme Commission Numbers, and Tissues and Buffer Systems used.

Locus	Abbrev.	E.C. No.	Tissue	Buffer System
Aspartate aminotransferase-1	AAT–1	2.6.1.1	muscle	Poulik
Aspartate aminotransferase-2	AAT-2	2.6.1.1	muscle	Poulik
Creatine kinase	CK	2.7.3.2	muscle	TC 6.7
Esterase	EST	3.1.1.1	liver	Poulik
Glucose-6-phosphate isomerase	GPI	5.3.1.9	muscle	Poulik
Glyceraldehyde-3-phosphate dehydrogenase	G-3-PD	1.2.1.12	liver	TC 6.7
Glycerol-3-phosphate dehydrogenase (NAD+)	GPD	1.1.1.8	liver	TC 6.7
Isocitrate dehydrogenase	IDH	1.1.1.42	muscle	TC 6.7
Lactate dehydrogenase-1	LDH-1	1.1.1.27	liver	TC 6.7
Lactate dehydrogenase-2	LDH-2	1.1.1.27	liver	TC 6.7
Malate dehydrogenase-1	MDH-1	1.1.1.37	liver	TC 6.7
Malate dehydrogenase-2	MDH-2	1.1.1.37	liver	TC 6.7
Malate dehydrogenase (NADP+) ("malic enzyme")	ME	1.1.1.40	muscle	Poulik
Peptidase-A	PEP-A	3.4.11.13	liver	Poulik
Peptidase-B	PEP-B	3.4.11.13	liver	Poulik
Peptidase-S	PEP-S	3.4.11.13	liver	Poulik
Phosphoglucomutase	PGM	5.4.2.2	muscle	Poulik
Triose-phosphate isomerase	TPI	5.3.1.1	muscle	TC 6.7

of the Andes from southern Colombia to central Ecuador (Fig. 2). In addition, *H. larinopygion* occurs at elevations of 2200–3300 m in the Cordillera Central of Colombia north to the Departamento de Antioquia (J.D. Lynch, pers. comm.).

HYLA PACHA NEW SPECIES

FIG. 3

Holotype.—KU 202762, an adult male, from 11.2 km (by road) west-southwest of Plan de Milagro (03°03'S, 78°08'W), 2350 m, Provincia de Morona-Santiago, Ecuador, one of a series collected on 12 March 1984 by William E. Duellman and David M. Hillis.

Paratypes.—KU 202760–61 collected with the holotype; KU 202763 from 12.4 km (by road) west-southwest of Plan de Milagro, 2225 m, Provincia de Morona-Santiago, Ecuador, obtained on 12 March 1984 by David M. Hillis.

Diagnosis.—This large species (females to 66.5 mm snout-vent length) differs from other members of the group by having a dark brown dorsum with orange flecks (cream in preservative) and bold black and cream mottling on the venter. *Hyla pacha* differs further from all species in the group, except *H. larinopygion* and *H.* sp. A, by having small, triangular calcars. *Hyla larinopygion* has a uniformly brown dorsum and black and blue bars on the flanks, whereas in *H.* sp. A the dorsum is brown with narrow, transverse black lines and the flanks are brown with large cream spots. The only other species in the group having orange on the dorsum are *H. pantosticta* and *H. sarampiona*. The former has many distinct, small, round, orange spots on all dorsal surfaces and the flanks and is unique in having areolate skin on the dorsum. *Hyla sarampiona* has a pale olive dorsum with small orange spots; the venter is black.

Description.—Body robust; head about as broad as long, as wide as body; head width 31.6–33.1 ($\bar{x}$=32.3, n=4) percent of snout-vent length; head length 32.1–34.3 ($\bar{x}$=32.9, n=4) percent of snout-vent length; length of snout greater than diameter of eye; snout in dorsal view acutely rounded, in profile bluntly rounded; canthus round; loreal region concave; lips not flared; nares slightly protuberant, directed anterolaterally at point posterior to anterior

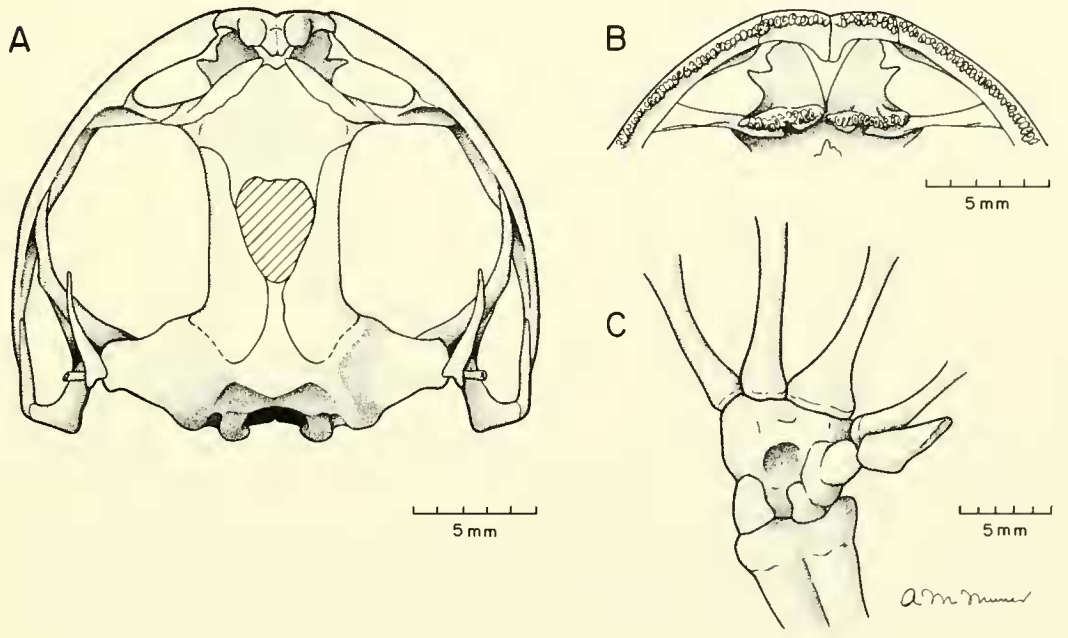

Fig. 1. Osteology of *Hyla lindae*, KU 155477, female, 64.5 mm SVL: A. Dorsal view of skull; B. Ventral view of anterior part of skull; C. Palmar view of right carpus.

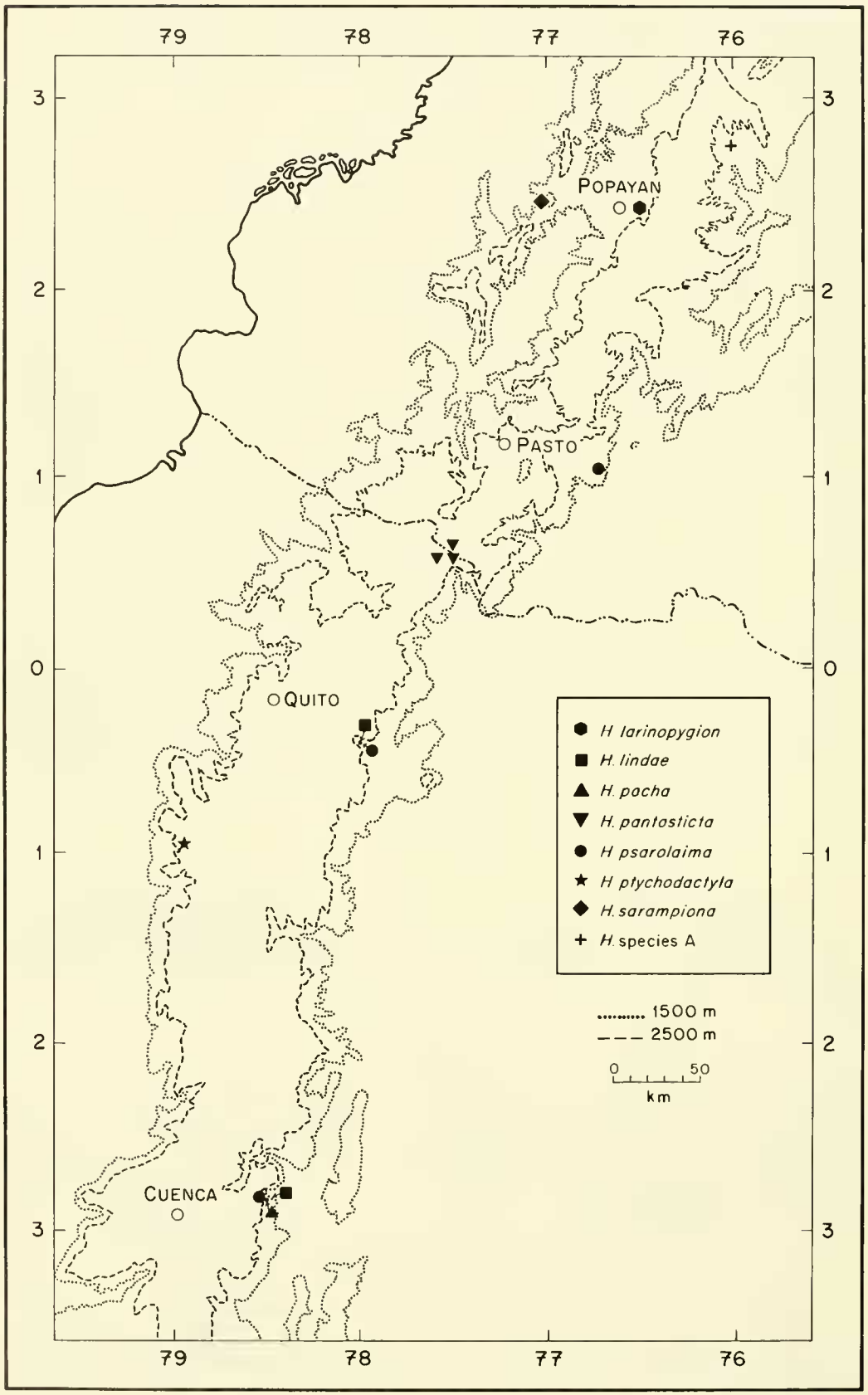

Fig. 2. Distribution of species in the *Hyla larinopygion* group in Ecuador and southern Colombia.

Fig. 3. Holotype of *Hyla pacha*, KU 202762, male, 58.0 mm SVL.

margin of lower jaw; internarial region barely depressed; top of head flat; interorbital distance noticeably wider than eyelid; eye moderately large, prominent; tympanum vertically ovoid, separated from eye by distance greater than twice length of tympanum; tympanic annulus distinct; supratympanic fold heavy, sigmoid, obscuring upper part of tympanum; post-tympanic fold heavy beginning under supratympanic fold, extending to angle of jaw, obscuring posterior edge of tympanum. Forearm robust; row of prominent tubercles along ventrolateral edge of forearm; fingers long, bearing large, round discs; width of disc on third finger twice length of tympanum; relative lengths of fingers 1<2<4<3; fingers webbed basally; webbing formula for outer fingers II2—3III3—3IV; subarticular tubercles large, round, none bifid; supernumerary tubercles large, round, in two rows on proximal segments; palmar tubercle large, bifid; prepollical tubercle large, elliptical; nuptial excrescences absent. Hind limb moderately robust; tibia length 48.5–52.5 ($\bar{x}$=50.2, n=4) percent of snout-vent length; foot length 47.5–50.3 ($\bar{x}$=48.4, n=4) percent of snout-vent length; calcar present, small, triangular; tarsal fold absent; inner metatarsal tubercle large, elliptical; outer metatarsal tubercle moderately large, distinct, round; toes long, bearing discs only slightly smaller than those on fingers; relative lengths of toes 1<2<3=5<4;

toes about one-half webbed; webbing formula I2⁻—2⁺II1½—2½III2⁻—3⁻IV2½—1½V; subarticular tubercles large, round; supernumerary tubercles prominent, round, in two rows on proximal segments.

Skin on dorsum and flanks finely shagreened; skin on throat finely granular; skin on chest, belly, and proximal posteroventral surfaces of thighs coarsely granular; other surfaces smooth; anal opening directed posteroventrally at midlevel of thighs in males, posteriorly at upper level of thighs in female; dermal supra-anal flap long, transverse in males, absent in female; pair of vertically elongate tubercles below anal opening. Vomerine odontophores long, transverse, abutting medially, behind level of large, ovoid choanae, bearing 11–15 ($\bar{x}$=13.3, n=4) teeth; tongue broad, cordiform, shallowly notched posteriorly, barely free behind; vocal slits along posterior lingual margins of mandibles; vocal sac large, single, median, subgular.

Coloration in preservative: Dorsal surfaces of head, body, forearms, and shanks black with scattered, minute cream flecks; flanks black with two or three bold cream vertical or diagonal marks; all surfaces of thighs and upper arms, inner surfaces of forearms and tarsi, and dorsal surfaces of hands and feet black with cream bars; digits cream and black; all ventral surfaces black with bold cream mottling (Fig. 4A).

Coloration in life: Dorsum dark brown with metallic orange flecks; venter, flanks, and hidden surfaces of limbs brown and creamy white; iris olive-brown.

Measurements: The measurements of three males (mm with means in parentheses are followed by the measurements of one female: snout-vent length 58.0–60.8 (59.2), 66.5; tibia length 29.1–29.5 (29.3), 34.9; foot length 27.6–29.3 (28.3), 33.5; head width 18.9–19.9 (19.6), 21.5; head length 18.7–20.1 (19.3), 21.0; interorbital distance 5.9–6.5 (6.1), 6.2; internarial distance 4.9–5.4 (5.1), 5.4; eye-nostril distance 4.3–4.9 (4.6), 4.8; diameter of eye 5.5–6.0 (5.7), 6.0; diameter of tympanum 2.4–2.8 (2.6), 3.0.

Distribution and ecology.—This species is known from only two streams at elevations of 2225 and 2350 m on the Amazonian slopes of the Cordillera Oriental in central Ecuador. All individuals were active at night in cloud forest. Males were calling from the ground adjacent to, a boulder in, and a tree limb 2.5 m above, a cascading mountain stream. A female was on a frond of a tree fern 10 m above the base of a waterfall. The call is a three-noted whistle that is higher pitched than the three-noted call of *H. lindae*.

Etymology.—The specific epithet is a noun in apposition and is a patyronym for Patricia (Pacha) A. Burrowes, who worked with us in the cloud forests of Ecuador in 1984.

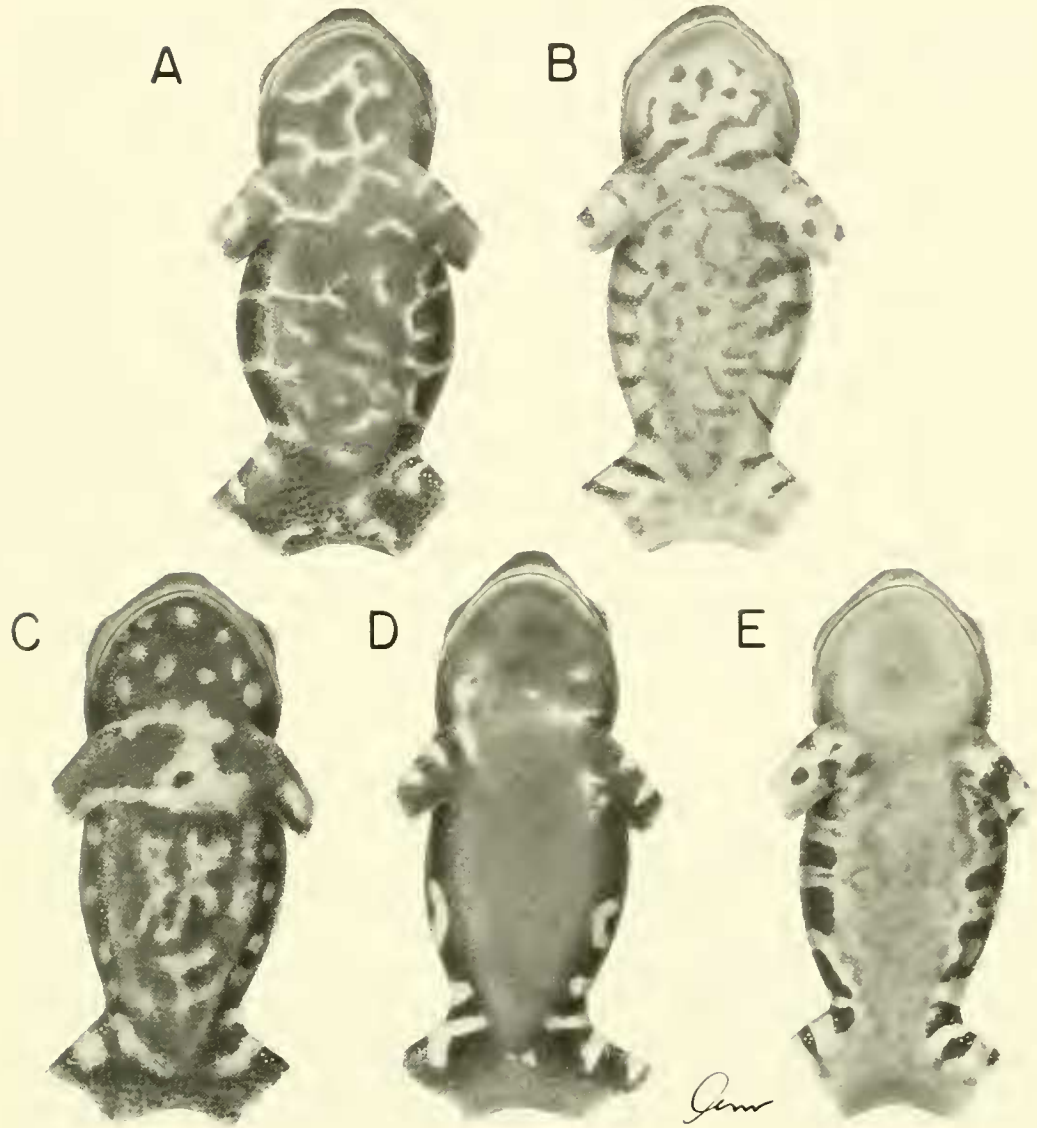

Fig. 4. Ventral color patterns in species in the *Hyla larinopygion* group: A. *H. pacha,* KU 202762; B. *H. larinopygion,* KU 144127; C. *H. pantosticta,* KU 190000; D. *H.* species A, KU 189598; E. *H. psarolaima,* KU 164313. The ventral surfaces of *H. lindae, sarampiona,* and *ptychodactyla* are unicolor, except that the latter has irregular pale spots on the throat.

HYLA PSAROLAIMA NEW SPECIES
FIG. 5

Holotype.—KU 164313, an adult male, from 11 km (by road) east-southeast of Papallacta (00°03'S, 78°08'W), 2660 m, Provincia de Napo, Ecuador, obtained on 22 March 1975 by Linda Trueb.

Paratypes.—KU 164314–15, 164316 (skeleton) from the type locality, collected on 23 March 1975 by William E. Duellman; KU 202727 from 26.2

km west-southwest of Plan de Milagro, 2640 m, Provincia de Morona-Santiago, Ecuador, obtained on 12 March 1984 by William E. Duellman; MCZ 109317–18 from between La Alegría and Sibundoy, 2410 m, Provincia de Napo, Ecuador, collected on 5 November 1984 by Robert Bleiweiss and Juan Carlos Matheus.

Referred specimens.—Four juveniles, KU 169582–85 from 35 km east of San Francisco, 1950 m, Departamento de Putumayo, Colombia, collected on 26 September 1974 by William E. Duellman and Linda Trueb.

Diagnosis.—This species differs from all other members of the group by having a creamy gray throat with brown and white flecks, gray venter with brown and cream spots, grayish brown dorsum with small brown and minute cream flecks, and a small tubercle on the heel. All other species in the group have a uniformly black venter (*H. lindae*, *sarampiona*, and species A) or boldly mottled black and cream or blue venters (*H. larinopygion*, *pacha*, and *pantosticta*). Dermal appendages are absent on the heels of *H. pantosticta* and *sarampiona*, whereas the other species in the group have small, triangular calcars, instead of an elongate tubercle as in *H. psarolaima*.

Fig. 5. Paratype of *Hyla psarolaima*, KU 164314, male, 55.4 mm SVL.

Description.—Body robust; head slightly longer than wide, as wide as body; head width 31.2–34.4 ($\bar{x}$=32.2, n=7) percent of snout-vent length; head length 31.9–34.4 ($\bar{x}$=32.7, n= 7) percent of snout-vent length; length of snout greater than diameter of eye; snout in dorsal view acutely rounded, in profile bluntly rounded, nearly truncate; canthus round; loreal region concave; lips not flared; nares slightly protuberant laterally, directed anterolaterally at point just posterior to anterior margin of lower jaw; internarial area barely depressed; top of head flat; interorbital distance greater than width of eyelid; eye moderately large, prominent; tympanum broadly ovoid, higher than long, separated from eye by distance 1.5 times length of tympanum; tympanic annulus distinct; supratympanic fold heavy, curved from posterior corner of eye to point above insertion of forelimb, obscuring upper part of tympanum; post-tympanic fold absent.

Forearm moderately robust; row of low tubercles on ventrolateral edge of forearm; fingers long, bearing moderately large, round discs; width of disc on third finger slightly greater than length of tympanum; relative lengths of fingers 1<2<4<3; fingers webbed basally; webbing formula for outer fingers II2^{+}—3^{+}III3^{+}—3IV; subarticular tubercles large, round, none bifid; supernumerary tubercles moderately large, round, in two rows on proximal segments; palmar tubercle large, flat, bifid; prepollical tubercle large, elliptical; nuptial excrescences absent. Hind limb moderately robust; tibia length 46.8–53.2 ($\bar{x}$=48.7, n=7) percent of snout-vent length; foot length 45.7–48.7 ($\bar{x}$=47.0, n=7) percent of snout-vent length; round, elongate, tubercle on heel; tarsal folds absent; ventral surfaces of tarsus with many low, diffuse tubercles; inner metatarsal tubercle moderately small, flat, elliptical; outer metatarsal tubercle not distinguishable; toes long, bearing discs slightly smaller than those on fingers; relative lengths of toes 1<2<3=5<4; toes about one-third webbed; webbing formula I2—2^{+}II2^{-}—3III2—3IV3—2V; subarticular tubercles large, round; supernumerary tubercles large, in single row on proximal segments, continuous with tubercles on tarsus.

Skin on belly and proximal ventral surfaces of thighs weakly granular; other surfaces smooth; anal opening directed posteroventrally at midlevel of thighs in males, posteriorly at upper level of thighs in females; dermal supra-anal flap long, transverse; pair of vertically elongate swellings ventrolateral to anal opening. Vomerine odontophores long, transverse, abutting medially, behind level of large, ovoid choanae, bearing 10–18 ($\bar{x}$=13.2, n=7) teeth; tongue broadly cordiform, shallowly notched posteriorly, barely free behind; vocal slits extending from midlateral base of tongue to angles of jaws; vocal sac single, median, subgular.

Coloration in preservative: Dorsal surfaces of head, body, shanks, and forearms brown with faintly darker brown flecks and scattered minute cream flecks (two females with narrow, irregular, transverse tan lines); markings on forearms and shanks in form of transverse bars; flanks dark brown with 3–5

vertical cream bars; all surfaces of upper arms and thighs, inner surfaces of forearms and tarsi, and dorsal surfaces of inner two fingers and inner three toes cream with black vertical bars; throat tan with small dark brown and cream flecks (fine cream reticulation in one female and two longitudinal cream bars in one female); belly grayish brown with diffuse dark brown spots and cream flecks (Fig. 4E).

Coloration in life: Dorsum grayish brown with dark brown and minute cream flecks (tan middorsal stripe in two specimens); flanks, upper arms, thighs, ventral shanks, and dorsal surfaces of feet cream with dark brown bars; throat, chest, and belly creamy gray with brown and cream flecks. Iris dull bronze with fine black reticulations.

Measurements: The measurements of four males are followed by those of three females (mm with means in parentheses): snout-vent length 53.6–55.6 (55.0), 58.1–63.4 (60.2); tibia length 24.8–26.5 (25.5), 28.5–32.2 (30.6); foot length 24.5–26.3 (25.5), 27.5–30.4 (28.7); head width 17.0–17.7 (17.5), 18.4–20.8 (19.7); head length 17.1–18.2 (17.8), 18.6–21.3 (20.0); interorbital distance 4.5–5.2 (5.1), 5.3–6.2 (5.9); internarial distance 4.4–4.9 (4.7), 5.0–5.6 (5.3); eye-nostril distance 5.0–5.6 (5.3), 5.4–5.6 (5.5); diameter of eye 5.0–5.6 (5.2), 4.8–6.2 (5.4); diameter of tympanum 2.3–3.0 (2.8), 2.9–3.2 (3.0).

Distribution and ecology.—*Hyla psarolaima* is known from cloud forests at elevations of 1950–2660 m on the Amazonian slopes of the Cordillera Oriental in southern Colombia and Ecuador. Most individuals were found on stems and branches of bushes near, or over, streams in cloud forest at night. Two females were in terrestrial bromeliads by day.

Etymology.—The specific name is derived from the Greek *psaros* meaning speckled and the Greek *laimos* meaning throat; the name is used in reference to the brown and cream flecks on the throat.

Remarks.—The specimens from Colombia and Papallacta, Ecuador, were referred to *H. larinopygion* by Duellman and Altig (1978).

Hyla ptychodactyla new species

Fig. 6

Holotype.—KU 209780, an adult male, from Pilaló (00°57'S, 79°02'W), 2320 m, Provincia de Cotopaxi, Ecuador, obtained in July 1987 by Giovanni Onore.

Paratopotypes.—KU 209781, MHNG 18715, 18724 (2 specimens), all collected by Giovanni Onore.

Diagnosis.—This species differs from all other members of the group by having pale spots on the throat, mottled black and tan dorsum, a conical tubercle on the heel, and a pale blue iris in life. All other species in the group have either a uniformly black venter (*H. lindae, sarampiona*, and species A),

Fig. 6. *Hyla ptychodactyla* from Pilaló, Provincia de Cotopaxi, Ecuador. Photo courtesy of Luis A. Coloma R.

boldly mottled black and cream or blue and cream venters (*H. larinopygion, pacha,* and *pantosticta*), or gray venter with brown and cream spots (*H. psarolaima*). Dermal appendages are absent on the heels of *H. pantosticta* and *sarampiona*; an elongate tubercle is present on the heel in *H. psarolaima*, and small, triangular calcars are present in the other species in the group. *Hyla ptychodactyla* is unique among Andean hylids in having a pale blue iris in life.

Description.—Body robust; head as long as wide, about as wide as body; head width 32.2–34.0 ($\bar{x}$=32.8, n=5) percent of snout-vent length; head length 32.0–34.0 ($\bar{x}$=33.1, n=5) percent of snout-vent length; length of snout less than diameter of eye; snout in dorsal view truncate, in profile bluntly rounded; canthus round; loreal region concave; lips not flared; nares barely protuberant laterally, directed anterolaterally at level of anterior margin of lower jaw; internarial area slightly depressed; top of head flat; interorbital distance greater than width of eyelid; eye moderately large, prominent; tympanum nearly round; separated from eye by distance 1.5 times length of tympanum; tympanic annulus distinct; supratympanic fold heavy, extending from posterior corner of eye to point above insertion of forelimb, obscuring upper part of tympanum; post-tympanic fold moderately heavy, beginning under supratympanic fold, extending to angle of jaw, obscuring posteroventral edge of tympanum.

Forearm moderately robust; ulnar tubercles absent; fingers long, bearing moderately large, round discs; width of disc on third finger slightly greater than length of tympanum; relative lengths of fingers 1<2<4<3; fingers

webbed basally; webbing between Fingers **I** and **II** vestigial; webbing formula for outer fingers **II**2—(3⁻–3)**III**(3⁻–3)—(2–2½)**IV**; subarticular tubercles large, round; supernumerary tubercles, large, subconical, in two rows on proximal segments; palmar tubercle large, flat, bifid; prepollical tubercle large, elliptical; nuptial excrescences absent. Hind limb moderately robust; tibia length 46.9–49.0 ($\bar{x}$=47.8, n=5) percent of snout-vent length; foot length 45.5–47.0 ($\bar{x}$=46.2, n=5) percent of snout-vent length; heel bearing blunt, conical tubercle; tarsal tubercles, tarsal fold, and outer metatarsal tubercle absent; inner metatarsal tubercle moderately latge, flat, ovoid, visible from above; toes long, bearing discs nearly as large as those on fingers; relative lengths of toes 1<2<3<5<4; toes about two-thirds webbed; webbing extending as lateral flaps onto bases of discs; webbing formula **I**(1–1½)—(1⁻–2)**II**1—(2⁻–2)**III**(2⁻–2)—(2½–3⁻)**IV**(2½–3⁻)—(1–1½)**V**; subarticular tubercles large, round; supernumerary tubercles low, round, in single row on proximal segments.

Skin on dorsum and flanks finely shagreened; skin on throat finely granular; skin on belly and proximal ventral surfaces of thighs coarsely granular; other surfaces smooth; anal opening directed posteroventrally at midlevel of thighs in males, posteriorly at upper level of thighs in female; dermal supra-anal flap long, transverse; pair of vertically elongate swellings lateral to anal opening. Vomerine odontophores long, transverse, abutting medially, behind level of large, round choanae, bearing 11–15 ($\bar{x}$=13.1, n=5) teeth; tongue round, not free behind; vocal slits curved from lateral base of tongue toward angles of jaws; vocal sac single, median, subgular.

Coloration in preservative: Dorsal surfaces of head and body dull reddish brown and black; pattern on head and body of holotype consisting of irregular, transverse black markings; female paratype dull brown with faint dark flecks; other specimens having intermediate types of patterns, but one with faint, narrow, pale middorsal line. Flanks uniform black (3 specimens) or with reddish brown extensions of dorsal ground color (2 specimens); groin and proximal surfaces of thighs black; rest of thighs black with 1–3 transverse pale bars on all but ventral surfaces. Forearms, shanks, tarsi, fingers, and toes with black and reddish brown transverse marks—2 or 3 black bars on forearms, 3 or 4 on shanks, 2 or 3 on tarsi. Venter black with large, irregular cream spots on throat (also on chest of female).

Coloration in life: Dorsum orange-tan to reddish brown with black markings (minute orange-tan flecks enclosed in black markings); venter black with cream spots on throat; iris pale blue.

Measurements: The measurements of four males (mm with means in parentheses) are followed by those of the single female: snout-vent length 65.0–67.5 (65.9), 77.3; tibia length 30.5–32.5 (31.7), 36.3; foot length 29.6–30.9 (30.5), 35.8; head width 21.2–23.0 (21.8), 24.9; head length 21.4–23.0 (22.0), 24.7; interorbital distance 8.0–8.2 (8.1), 8.7; internarial

distance 4.9–5.8 (5.2), 6.0; eye-nostril 5.2–5.5 (5.3), 5.5; diameter of eye 6.2–6.4 (6.3), 6.5; diameter of tympanum 3.4–4.0 (3.6), 4.0.

Tadpoles.—Although the largest tadpole has a body length of 27.2 mm and a total length of 78.4 mm, it has not yet developed hind limb buds. The following description is based on KU 180360.

Body length 20.4 mm; total length 64.9 mm; body depressed, wider than deep, ovoid, widest just posterior to eyes; snout bluntly rounded in dorsal view and in profile; eyes small, widely separated, directed dorsolaterally; nostrils about midway between eyes and snout; spiracle sinistral, its opening directed posterodorsally at level of midline about two-thirds length of body; cloacal tube short, dextral. Caudal musculature robust, gradually tapering to pointed tip just short of tip of acutely rounded tail; dorsal and ventral caudal fins about equal in depth; at midlength of tail depth of each fin slightly shallower than depth of caudal musculature.

Mouth large, directed ventrally, completely bordered by single row of small, pointed papillae; larger, conical papillae in lateral folds; beaks slender, finely serrate; upper beak forming broad arch; lower beak broadly V-shaped; seven upper and eight lower rows of denticles (one more upper and two more lower rows in largest tadpole); innermost three upper rows, and innermost lower row narrowly interrupted medially.

In preservative, body and caudal musculature brown; fins translucent. In life, body gray flecked with black; caudal musculature finely reticulated with brown; golden streak along top of caudal musculature edged with black stripe; fins colorless except for fine brown reticulation; iris pale green.

Distribution and ecology.—The species is known only from the type locality in disturbed cloud forest. Adults were found by day by tracing their calls, a series of tick-like notes, to frogs under deep moss along seepage areas by streams. The tadpoles were found at night in pools in a stream in a clearing.

Etymology.—The specific name is derived from the Greek *ptychos* meaning fold or flap and the Greek *dactylos* meaning toe; the name alludes to the dermal flaps on either sides of the toes that are extensions of the webbing.

Remarks.—The type locality is a small village on the Pacific slopes of the Andes; it is 78 km east of Quevedo on the road to Latacunga. The tadpoles of this species were discovered by John D. Lynch in July 1970 and were subsequently collected by him again in 1977, at which time he succeeded in raising two individuals, one to Stage 42 with a snout-vent length of 32.9 mm and a tail stub 33.4 mm long, and the other to metamorphosis with a snout-vent length of 31.0 mm.

Key to Adults of the *Hyla larinopygion* Group

1. Venter uniformly or predominately black 2
   Venter mottled black and white or blue, or brownish gray with brown spots

and cream flecks 5

2. Throat uniformly black; no pale marks on flanks or hidden surfaces of limbs ..... *H. lindae*
   Throat black with orange or cream flecks; hidden surfaces of limbs with red spots or cream bars 3
3. Dorsum pale olive-brown with small orange spots; hidden surfaces of limbs with red spots ..... *H. sarampiona*
   Dorsum brown with irregular black marks; hidden surfaces of limbs black with pale bars 4
4. Digital discs dark; irregular, large pale spots on throat ..... *H. ptychodactyla*
   Digital discs pale; small pale flecks on throat ..... *H.* species A
5. Venter brownish gray with dark brown spots and cream flecks; dorsum brown with small, dark brown and cream flecks ..... *H. psarolaima*
   Venter mottled dark brown or black and white or blue; dorsum uniform brown or with orange (cream in preservative) spots or flecks 6
6. Dorsum uniform brown; flanks and hidden surfaces of thighs with bold black and blue (cream in preservative) vertical bars ..... *H. larinopygion*
   Dorsum brown or black with orange (cream in preservative) spots or flecks; flanks spotted, or barred 7
7. Dorsum brown with small orange flecks; throat and belly dark brown with bold cream mottling; hidden surfaces of limbs black with narrow, vertical, cream bars; discs on digits cream and black ..... *H. pacha*
   Dorsum and throat black with orange spots; belly black with white mottling; hidden surfaces of limbs black with orange spots; discs on digits yellow ..... *H. pantosticta*

GENETIC DIVERGENCE AND PHYLOGENETIC RELATIONSHIPS

Genetic divergences among the species in the *Hyla larinopygion* group were considerable and ranged from 0.329 to 1.242 *D* (Table 3, Fig. 7). Interestingly, the two most similar species genetically are the two described herein from the Amazonian slopes of the Andes in Ecuador. We collected these two species at elevations separated by only 290 meters on the same slope in central Ecuador. However, they are quite distinct morphologically and genetically.

The allozymic data were used to construct a proposed phylogeny of the members of the group (Fig. 8). For this analysis, we identified symplesiomorphic electromorphs at 11 of the 18 loci by using a wide diversity of outgroups (Tables 1, 4). Variation at two of the loci (IDH and ME) suggest that *H. lindae* is the sister species to the remaining taxa; this permitted the use of *H. lindae*

TABLE 3. Modified Nei's genetic distances (Hillis, 1984) among species in the *Hyla larinopygion* group.

Species	*H. lindae*	*H. larinopygion*	*H. psarolaima*	*H. pacha*
H. pantosticta	0.703	0.519	0.492	0.693
H. lindae	—	0.987	1.066	1.242
H. larinopygion	—	—	0.618	0.618
H. psarolaima	—	—	—	0.329

as a functional outgroup (Watrous and Wheeler, 1981; Farris, 1982) to the remaining species. Similarly, variation at the EST locus suggests that *H. lindae* and *H. pantosticta* can be considered as functional outgroups to the other three species. By using this information, it was possible to code transformation series for all 18 loci, although more than one equally parsimonious alternatives is possible for MDH-1 (this locus is diagnostic for each of the species). The resulting cladogram (Fig. 8) contains no homoplasy.

Morphologically, *H. psarolaima* and *H. larinopygion* are the most similar species in the group, a fact that resulted in confusion of the two species in the past (Duellman and Altig, 1978). However, these taxa apparently are not sister species; the electrophoretic data indicate that *H. psarolaima* is more closely related to the morphologically distinct *H. pacha* than to the morphologically similar *H. larinopygion*. These data suggest that *H. pacha* has diverged farther from their common ancestor, both morphologically and allozymically, than has *H. psarolaima*.

Although most of the morphological differences among species in this group are autapomorphic, some morphological characters are consistent with the phylogeny based on allozymes. Three of the species (*H. larinopygion, pacha,* and *psarolaima*) have distinct vertical light and dark bars on the their flanks and limbs. These three species form a monophyletic group according to the allozymic data, although this part of the tree is supported by only one electromorphic change (Fig. 8). *Hyla lindae* and *pantosticta* (also *H. sarampiona,* for which allozymic data are not available) have pale discs on the digits, which distinguish them from the branch of the tree containing *H. larinopygion, pacha,* and *psarolaima*. Among the species for which allozymic data are available, *H. lindae* is unique in having a plain, dark venter, a character shared with *H. sarampiona* and *H.* sp. A. The available morphological data are insufficient to determine the relationships of *H. sarampiona* and *H.* sp. A, but they seem to be more like *H. lindae* than the other species in the group. However, as noted for *H. larinopygion* and *psarolaima*, phenetic similarity of color patterns may be misleading.

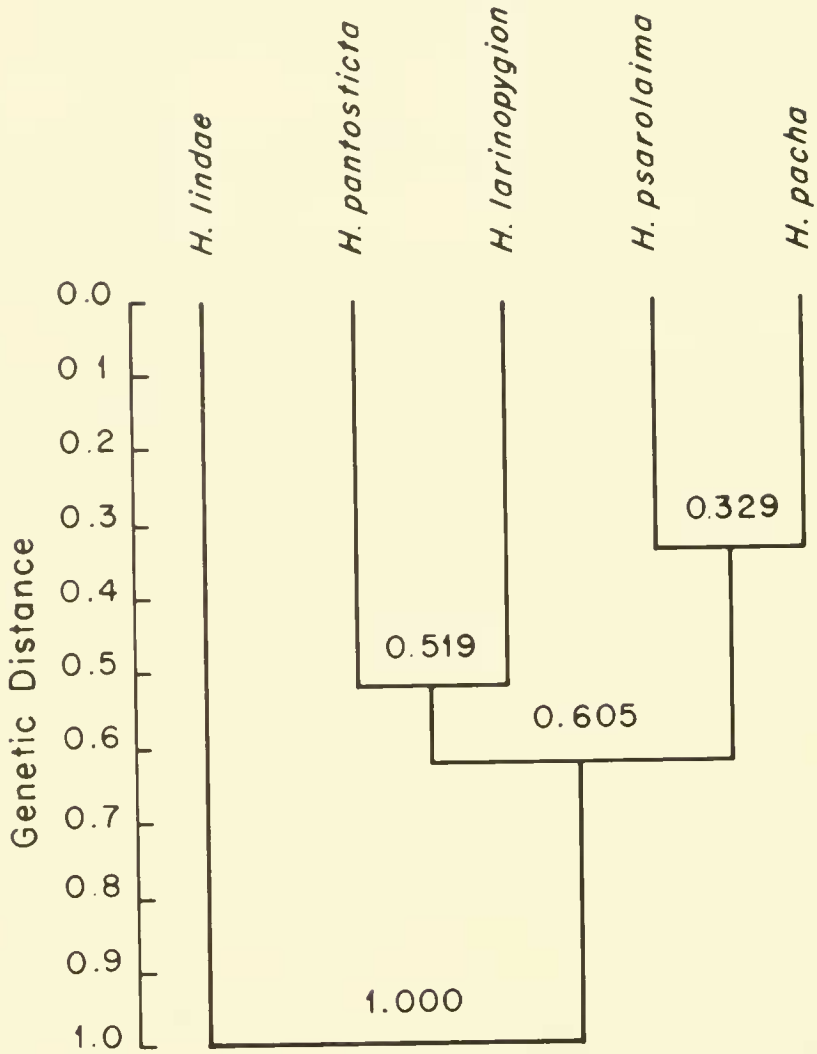

Fig. 7. Phenogram of modified Nei's genetic distances (Hillis, 1984) among five taxa in the *Hyla larinopygion* group.

Differences exist in the configuration of the caudal fins and in the rows of labial denticles in the tadpoles. The tadpole of *H. lindae* has relatively deep caudal fins and six upper and eight lower rows of denticles. The tadpole of *H. pantosticta* has very shallow fins and four upper and six lower rows of denticles. Tadpoles from a stream near localities where *H. pacha* and *psarolaima* were found are like those of *H. lindae* but have eight upper and nine lower rows of denticles; these tadpoles may belong to either of those was

TABLE 4. Electromorphs of the *Hyla larinopygion* group. Alleles found in both the ingroup and the outgroup are indicated under the outgroup; if no alleles could be found in common between the groups, an "x" is shown for the outgroup.

Locus	*larinopygion*	*lindae*	*pacha*	*pantosticta*	*psarolaima*	Outgroup
AAT-1	e (1.00)	d (1.00)	b (0.25) c (0.75)	a (0.50) d (0.50)	c (1.00)	x
AAT-2	a (0.50) b (0.50)	b (1.00)	b (1.00)	b (1.00)	b (1.00)	b
CK	a (1.00)	a (1.00)	a (1.00)	a (1.00)	a (1.00)	x
EST	b (1.00)	a (1.00)	b (1.00)	a (1.00)	b (1.00)	a
GPI	c (1.00)	a (0.83) b (0.17)	d (1.00)	c (1.00)	d (1.00)	a
G-3-PD	a (1.00)	a (1.00)	a (1.00)	a (1.00)	a (1.00)	x
GPD	a (1.00)	a (1.00)	a (1.00)	a (1.00)	a (1.00)	x
IDH	b (1.00)	a (1.00)	b (1.00)	b (1.00)	b (1.00)	a
LDH-1	b (1.00)	b (1.00)	b (1.00)	a (1.00)	b (1.00)	b
LDH-2	b (1.00)	a (1.00)	b (1.00)	b (1.00)	b (1.00)	b
MDH-1	b (1.00)	c (1.00)	a (1.00)	e (1.00)	d (1.00)	x
MDH-2	a (0.50) e (0.50)	d (1.00)	c (1.00)	b (1.00)	b (1.00)	d
ME	b (1.00)	a (1.00)	b (1.00)	b (1.00)	b (1.00)	a
PEP-A	a (1.00)	a (1.00)	a (1.00)	a (1.00)	a (1.00)	a
PEP-B	c (1.00)	a (1.00)	b (1.00)	a (1.00)	a (1.00)	x
PEP-S	c (1.00)	c (1.00)	b (1.00)	c (1.00)	a (1.00)	c
PGM	a (1.00)	b (0.33) c (0.67)	a (1.00)	a (1.00)	a (1.00)	a
TPI	c (1.00)	a (0.83) b (0.17)	b (1.00)	b (1.00)	b (1.00)	x

species or be a variant of *H. lindae*. Tadpoles of *H. ptychodactyla* have shallow fins and seven upper and eight lower rows of denticles.

Additional specimens of adults are needed for skeletal preparations, and tadpoles of all of the taxa need to be identified before the relationships of all of the species may be determined. These frogs seem to be extremely localized in their distributions, and we suspect that several additional species await discovery. Consequently, a biogeographic synthesis is premature. However, the localized distributions in cloud forests in all three major cordilleras in the

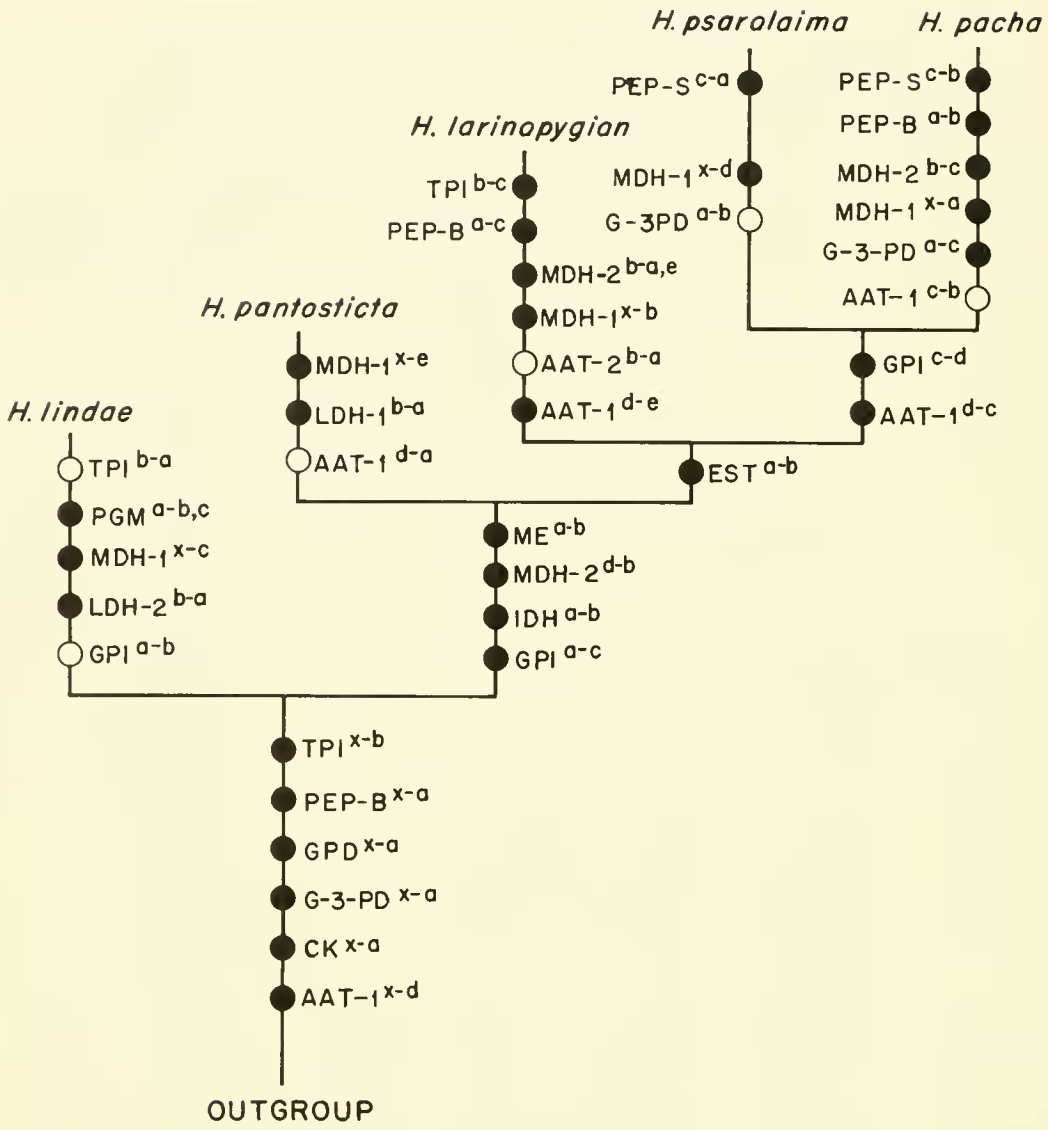

Fig. 8. Cladogram of hypothesized phylogenetic relationships among five species in the *Hyla larinopygion* group based on allozymic data. Solid circles mark the appearance and fixation of new alleles (e.g., GPI^{a-c} marks the evolution of allele *c* from allele *a* at the GPI locus). Open circles mark the appearance of new alleles without fixation (i.e., the ancestral allele is retained in a polymorphic state). Ancestral alleles represented by *x* could not be determined in the analysis.

northern Andes suggest that the pattern of speciation and biogeography may support Duellman's (1982) hypothesis of alternate compression and expansion of cloud forests during the Quaternary.

ACKNOWLEDGMENTS

The collection of these elusive frogs was aided by the efforts of Patricia A. Burrowes, John E. Simmons, and Linda Trueb. Field work in South America

supported by grants (DEB 74-02998 and 82-19388) from the National Science Foundation to W. E. Duellman. Laboratory work was supported by grants (BSR 86-57640 and 87-96293) from the National Science Foundation to David M. Hillis. Collecting permits for Colombia were issued by Jorge I. Hernández-C. of the Instituto de los Recursos Naturales Renovables, and for Ecuador by Sergio Figueroa and Abel Tobar V. of the Ministerio de Agricultura y Ganaderia. We are grateful to Volker Mahnert, José E. Rosado, and Pedro M. Ruíz-C. for the opportunity to examine material in their care, to Juan M. Renjifo for the tissues of one species, to Luis A. Coloma R. and John D. Lynch for information on the distribution and ecology of some species, to Rafael de Sá for translating the resúmen, and to Anne M. Musser for preparing the illustrations.

RESUMEN

El grupo de especies de *Hyla larinopygion* contiene ocho especies conocidas que habitan el bosque nebuloso de las laderas de los Andes de Ecuador y Colombia, a alturas entre 1900 y 3300 m. Se describen tres nuevas especies, *H. pacha* y *H. psarolaima* de las laderas amazónicas de los Andes ecuatorianos y *H. ptychodactla* de las laderas pacíficas de los Andes ecuatorianos. Se obtuvo información aloenzimatica de cinco especies y mediante electrofóresis en geles de almidón se registraron 18 loci diferentes. Basados en los electromorfos, el cladograma más parsimonio indica a *H. lindae* como la especie hermana a las demas especies y también a grupo a *H. larinopygion, psarolaima,* y *pacha* en un mismo clade que tiene a *H. pantosticta* como especie hermana. El cladograma también es soportado por caracteristicas del patrón de coloración.

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APPENDIX 1: SPECIMENS EXAMINED

Tissues for allozymic analysis were obtained from those numbers designated by an asterisk.

Hyla larinopygion.—COLOMBIA: Cauca; Quebrada Santa Teresa, 2200 m, KU 144127–28. [Also see Materials and Methods*].

Hyla lindae.—ECUADOR: Morona-Santiago; 21.6 km WSW Plan de Milagro, 2350 m, KU 202728*–29*; 23.3 km WNW Plan de Milagro, 2125 m, KU 202730–31*; 202966 (tadpoles). Napo: 11 km ESE Papallacta, 1660 m, KU 155475, 155477 (skeleton), 155523 (tadpoles), 164402, 166210 (tadpoles), 171188 (tadpoles).

Hyla pacha.—ECUADOR: Morona-Santiago: 11.2 km WSW Plan de Milagro, 2350 m, KU 202760*–61*, 202762; 12.4 km WSW Plan de Milagro, 2225 m, KU 202763.

Hyla pantosticta.—COLOMBIA: Nariño: La Victoria, 2700 m, KU 140385. ECUADOR: Carchí: 0.5 km S Santa Bárbara, KU 190000–01. Napo: 1 km E Santa Bárbara, 2520 m, KU 202733*; 12 km E Santa Bárbara, 2550 m, KU 202965 (tadpole); 18 km E Santa Bárbara, KU 202732.*

Hyla psarolaima.—COLOMBIA: Putumayo: 35 km SE San Francisco, 1950 m, KU 169582–85. ECUADOR: Morona-Santiago: 26.2 km WSW Plan de Milagro, 2640 m, KU 202727.* Napo: Between La Alegría and Sibundoy,

2410 m, MCZ 109317–18; 11 km ESE Papallacta, 2660 m, KU 164313–15, 164316 (skeleton).

Hyla ptychodactyla.—ECUADOR: Cotopaxi: Pilaló, 2320 m, KU 132553–54 (tadpoles), 180360 (tadpoles), 180361–62 (young), 209780–81, MHNG 18715, 18724 (2).

***Hyla* sp. A**.—COLOMBIA: Cauca: Paez, 34.5 km between Belalcazar and Tacueyo, 2400 m, KU 189598.